NATIONAL ACADEMY OF SCIENCES

CHARLES HASKELL DANFORTH

1883—1969

A Biographical Memoir by

BENJAMIN H. WILLIER

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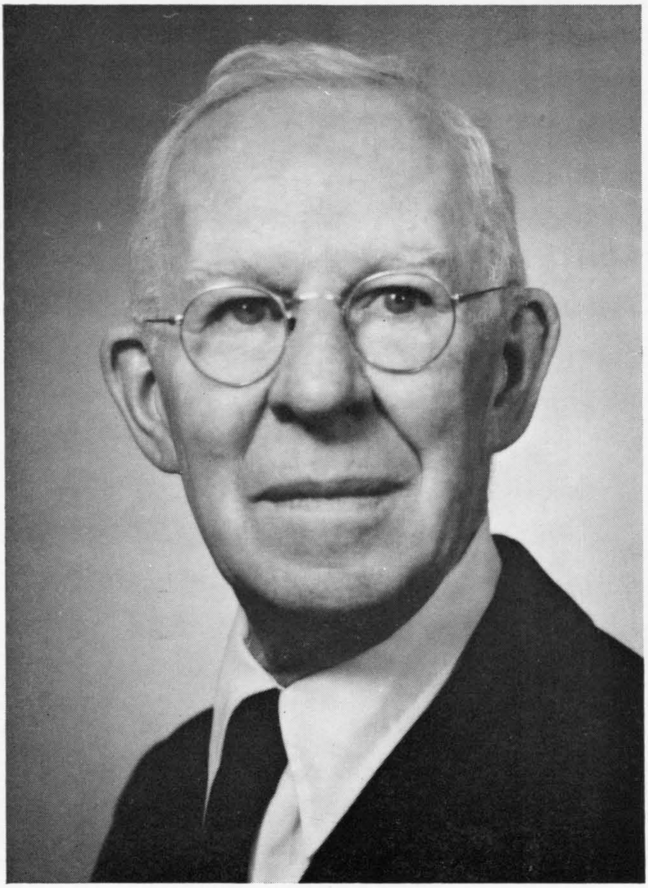

C. H. Danforth

CHARLES HASKELL DANFORTH

November 30, 1883–January 10, 1969

BY BENJAMIN H. WILLIER *

CHARLES HASKELL DANFORTH left not only a published record of sixty years (1907–1967) of scientific articles but also an autobiographical sketch (a typewritten copy of thirty pages dated March 1948 which was deposited in the files of the Home Secretary of the National Academy of Sciences) that tells the story of "facts not usually printed in biographical reference books," for example, such items as home life and occupations, schooling, and development of special interests. This sketch was written merely for "atmosphere," and so that his "possible biographer need do little more than condense and paraphrase—which somehow reminds me of one of my earliest observations that it takes many buckets of sap to make a small cup of syrup." It is of interest here to note that, in a fire which destroyed the Danforth home in 1939, there was lost "a notebook in which I began during high school days to develop, point by point, what I hoped would be a satisfactory and integrated philosophy and code for living."

* Dr. Willier died December 3, 1972, before the processing of his manuscript had been completed. The final version of this memoir owes a good deal to the constructive criticisms and/or valuable comments of Leslie C. Dunn, Roman O'Rahilly, Curt Stern, and Sewall Wright, the last named providing the evaluation of Danforth's pioneer paper on frequency of mutation in man. Special credit is due Curt Stern who assumed the responsibility for the final editing of the memoir.

No one who knew Charles Danforth personally and has visited the region of his birth in his native state can imagine for him any other birthplace. He was born on the last day of November 1883 on "a farm just over the Oxford line and about three miles from Norway village" in Maine, the Pine Tree State ("Old Dirigo"). The natural environment in and around Norway to the horizon is a typical postglacial landscape near the southern margin of the Wisconsin Continental glacier, a result of the last great ice age (10,000–15,000 years ago) in the Pleistocene epoch. It is a picturesque region made up of forests, freshwater lakes and ponds, hills and valleys, and springs and streams interspersed with agricultural farmlands. The many forests are of mixed character, with white pine and other conifers, and deciduous trees such as white birch, sugar maple, and oak. And there is the poet's rhodora whose "beauty is its own excuse for being." The hills, seven of them, range in height from Pikes Hill (870′) to Merrill Hill (1,243′) in the town of Norway. Indeed, our biographee had a gentle face and personality akin to the landscape of the gentle hilltops, beloved forest green, quiet lakes and rippling brooks, and rustic simplicity of the farmland. Such was nature's scenic area that played a role in Danforth's development as a naturalist.

ANCESTRY

In telling words Danforth wrote: "Most New Englanders of colonial stock have much the same ancestral background and my own is quite typical of the group as a whole." So far as he had been able to learn it seemed probable that all of his immigrant ancestors were exclusively British (English, Scottish, Welsh, and possibly Irish). All of them reached America during the first half of the seventeenth century, some coming in the *Mayflower* and some in various small vessels. They spread along the coast from Plymouth to what is now southwestern Maine (Oxford, York, and Cumberland counties). The largest early concentrations of them were around Boston, Billerica, Salem, and Falmouth. Of these early arrivals a few may have returned to England; the majority, however, lived and died within two hundred miles of Boston. Danforth "thinks" that every one of his native American ancestors was born and died within the same radius. He writes: "As a group they were fairly representative of the large middle class whose members rarely distinguished themselves by any very appreciable deviation from the norm of their time and locale." Danforth lists fifty-seven names of these ancestors. Among them are Danforth (grandfather), Frost (maternal grandmother), Reed (grandmother), and Haskell (grandfather and mother). Further, "there are more names than there are chromosomes in a human germ cell, so it is quite possible that some of these lines are ancestral in name only." He was surprised to find only a low degree of consanguinity among his direct ancestors. To establish descent Danforth became a member of the Society of Mayflower Descendants about 1930.

The last of his ancestors to go from Massachusetts to Maine was his paternal grandfather, Asa Danforth, who having been licensed at Boston in 1820 to "practice physick and surgery" moved shortly thereafter to Norway, Maine, and there married a descendant of a *Mayflower* passenger, Abigail C. Reed, daughter of the first postmaster of the town. Asa Danforth practiced his profession in Norway for nearly sixty years and seems to have been a typically beloved old-time country doctor. It is said that he built the first woolen mill in the state and was engaged in a variety of town affairs. His fellow citizens evidently respected and trusted him, for he served a term in the state legislature. The couple had nine children, of whom James Danforth was the eighth child, the father of Charles, his brother (Francis) and two sisters (Ann and Sara). James Danforth's occupation included being a farmer, a commercial traveler, and caretaker of his father's property interests. He had considerable interest in ancient and colonial history as well as an appreciation of good writing. Moreover, in personal relations with his son Charles, James Danforth "employed good psychological techniques or perhaps better just normal common sense."

Charles Danforth's maternal grandfather was Charles Henry Haskell, a native of Westbrook, Maine, whose ancestors arrived on the *Mayflower*. He married Laura Diantha Frost, a descendant of the first settlers of the town of Norway, also passengers on the *Mayflower*. This grandfather was a farmer, and at times an agent for a cracker company, a road surveyor, and a minor town official. The couple had five children, all girls, the eldest of whom was Mary File Haskell, the mother of Charles. His mother had the usual high school education of that period and taught school for a while. Throughout her life she took an active interest in the local schools, participated in the activities of a literary club, and frequently served as chairman of church and other organizations. She "did not seek responsibility but took it seriously when it did come her way." As a mother she was sympathetic and solicitous—inclined to "drive" rather hard in the intellectual field. She had a sound but aggressive interest in the schools where Charles was a pupil.

By contrast, his grandmother Haskell "had the most 'character' in the group." A good voice, a good sense of humor, and a good memory made her interesting and stimulating. She had "angles," however, that were to be merely tolerated—her attitude toward life was more defiant than humble.

On June 24, 1914, Charles Haskell Danforth married Florence Wenonah Garrison, a teacher of science and a member of the Daughters of the American Colonists and the Society of Daughters of the American Revolution, who was a writer of delightful historical articles on the Smithsonian Institution.* The couple had three sons, Charles Garrison (biologist), Alan Haskell (lawyer), and Donald Reed (engineer). Mrs. Dan-

* See *American Heritage*, 15 (1963):26–27.

forth died in May 1968 about eight months prior to the demise of her husband, who himself died in the hospital on the Stanford University campus on January 10, 1969.

TO BE OR NOT TO BE—A NATURALIST

The total environment comprising wild nature and intellectual climate provided a setting into which Charles was born and developed into a young man. His first eight and a half years were spent mostly on the farm of his parents. As he grew older, he participated "at least vicariously" in most of the common activities of a typical agricultural farm, such as making hay and maple syrup and weeding the garden. More attractive, however, were "my abundant and very pleasant memories of this period [that] have rather strong emotional components [of] mingling evening twilights with slightly eery calls of frogs and whip-poorwills, the boom of nighthawks and lowing of distant cattle, the exhilaration of morning with sunshine on the tree tops, and myriad things of interest through the whole day." These early interests and observations appertained to each and every living thing whether plant or animal. Seemingly not one was overlooked—ranging from the speckled lily *(Lilium canadense)* and partridge berries to nighthawks and thrashers. "Seeing my first humming bird was an event, dampened a little by learning it was not a queen bee."

At seven years of age he entered primary school in Norway village where he lived with his grandparents, the Haskells—going home for weekends. Of this period he writes: "School matters do not loom large in my memories. It is the 'farm' and not the 'village' around which my memories center most vividly."

The aggregate of environmental conditions affecting his life and development changed for Charles in 1892. In that year his father sold the farm and took over the home and other holdings of grandfather Haskell in Norway, a village of "perhaps 2000 people." There was a "little island in the brook" on the old farm, however, that took a long time before "I became reconciled to relinquishing" it.

From this time on to 1897, a period of five years of "early days in Norway," his environment combined the main features of farm life, though on a reduced scale, and of life in a small manufacturing town. He participated in the work of the former as he did on the old farm and in "the diversion" of the latter. Charles did not lose any of his natural curiosity and deep interest in living objects. In fact, at about twelve years of age while botanizing in Norway, he found plants of the saxifrage family—known commonly as foam flower or false miterwort—that vary in color of the anthers, which is either a bright yellow or an orange red. This discovery of a clear-cut variation of a single character was either held in memory for ten years or, more likely, recorded in his notebook. It was not until 1911, three years after graduation from college, that this early observation was published under the title of "A Dimorphism in *Tiarella cordifolia*."

Although love of nature was primary, great books and distinguished naturalists were also influential in his decision whether or not to be a naturalist. Of singular influence were the famous volumes of Darwin, as the following quotation shows:

"A particularly memorable evening occurred in the summer of my eleventh or twelfth year. Several of us boys were rolling hoops around the square during a long summer twilight when my uncle Frank Danforth, passing by, called me to the sidewalk and gave me two books that he thought I 'might like to have.' They were the two volumes of Darwin's *Animals and Plants under Domestication* and the inscriptions on their flyleaves showed that they had long ago been presented to my grandfather Danforth by A. E. Verrill. These volumes proved fascinating reading and probably influenced me more than any other books I have ever read. They dealt with things with which I was familiar, and in a way that made a strong appeal to my imagination. The close observation and the type of reasoning displayed in the chapters, especially those dealing with the pigeon and dog, were highly stimulating. I read them with intense interest, reflected much on their contents, and observed my own animals more closely. My father, who had apparently not noticed these volumes before, also read them, but my mother mildly disapproved.

"Although at this time I had never heard of the National Academy of Sciences, three of its members were well known to me by name. They were C. O. Whitman, Sidney I. Smith, and A. E. Verrill, all of whom had attended the Norway High School ('Liberal Institute') with my father. Throughout life, my father's most intimate friend was the brother of Professor Smith and brother-in-law of Professor Verrill. So with a feeling of easy familiarity I wrote to Professor Verrill telling him that I expected to be a naturalist and asking for suggestions. He replied, in effect, 'Don't unless you can't help it.' At thirteen I thought I couldn't help it. How much of my subsequent history is due to the strength of this assumption, and how much to chance or lack of imagination, I can not say."

But why did Professor Verrill, a distinguished naturalist, discourage young Charles from becoming a naturalist? In an attempt to answer this question it is perhaps of significance "to recall that Verrill lived through practically the entire history of zoology in America, from the coming of Louis Agassiz in 1847, to the experimental period of the present century." The vogue in zoology had changed from taxonomy to comparative anatomy, then to adaptations and other zoological disciplines, and at the beginning of the twentieth century to experimental fields. Moreover, "Verrill maintained to the end of his life the importance of taxonomy as a necessary preliminary to this more specialized biological work," that is, to genetics and other experimental fields.*

At the age of fourteen another change came about for Charles—a move to a house on Pleasant Street where he was to live with his family for six years. The move in itself introduced no radical change in his life. His work consisted of the usual chores such as delivering milk, caring for lawn and garden, and all the usual phases of farming such as plowing, hoeing, and harvesting crops. These activities were commonly shared with his father. "I never received any pay for my work nor any explicit allowance—boys of my age and background felt themselves as much a part of their family in responsibilities as in other respects." There was no sense of oppression or lack of freedom. Charles took a special interest in selecting the best seeds for flower and vegetable gardens. He introduced into his neighborhood the then new strain of chickens known as "Rhode Island Reds." Experience in breeding them led him to conclude, "In general a poor specimen of a good strain is to be preferred to a good specimen of a poor strain (to which I might now take some exception)."

The change had decided advantages, for it made his contact with woods and fields even easier than before. Behind the house was a wooded tract belonging to his uncle and beyond that the lake, the "Great Pond" or Pennesseewassee Lake, streams, pastures, and swamps stretching off toward wilder, more alluring country.

Charles entered a high school with a long and distinguished background in promoting the "cause of education" and culture of the mind. In his life sketch Charles refers to his high school as "the lineal descendant of the Norway Liberal Institute." This phrase has unusual significance, since the Institute at the time

* See Biographical Memoir of Addison Emery Verrill, by Wesley R. Coe, National Academy of Sciences, *Biographical Memoirs,* 14 (1929):39.

of its greatest vigor was highly respected for its excellence. (Many such Liberal Institutes were established by the people in western Maine—in 1852 there were six of them in Oxford County and ten in York County. The purpose of their founding was "for promoting religion and morality, and for the education of the youth in such languages, and such of the liberal arts and sciences as the said Trustees shall direct.")

During its eighteen years of existence the Norway Liberal Institute was " a college-fitting school" of very high rank with "a brilliant record." Many of its students entered colleges and universities where they often graduated with high honors. Of its early graduates three were members of the National Academy of Sciences who were active pioneer leaders in the development of the life sciences in our universities. C. O. Whitman was the first director of the Marine Biological Laboratory at Woods Hole, Massachusetts, and first chairman of the Department of Zoology, University of Chicago; Addison E. Verrill was the first Professor of Zoology, Yale University; and Sidney I. Smith was Professor of Comparative Anatomy, Yale University. To this trio of distinguished Academicians the name of Charles H. Danforth was added in 1942—a grand total of *four* Norway Liberal Institute naturalists.

The Norway Liberal Institute was opened in 1847 as a self-supporting academy; it started with 174 pupils, a principal, and a corps of teachers of much ability and enterprise and was incorporated June 25, 1849. About 1865 "the village district purchased the Institute building and changed the name of the school to the one it bears today." *

Whether the Norway High School at the time Charles entered it was equal in educational capability to the Institute, he does not say, yet the influence of its forerunner remained strong for several decades. He tells of choosing the "classical

* See Charles F. Whitman, *A History of Norway, Maine, from the Earliest Settlements to the Close of the Year 1922* (Lewiston, Maine, 1924).

curriculum" without giving the choice any special thought. The courses included Latin, Greek, English, and mathematics. Of these, Latin and Greek were "especially pleasant." "The *Aeneid,* more than any other book, awakened an appreciation of epic sequences and lyric associations." While a passage of the *Aeneid* was running through his mind one morning as he was feeding the cows, it suddenly occurred to him that a part of the beauty of passages written in foreign languages is "that the words are not overladen with connotations and so stimulate rather than hinder the imagination."

Charles retained an interest in the classics in his high school years. In addition, these years were naturally ones of expanding interests and a time during which new acquaintances of influence were being made. One of the most important of these was apparently his teacher Walter Bacon. In his fifteenth or sixteenth summer Charles wrote: "While walking near the pond one day, I saw a man crouching on the shore and intently looking into the water. As I approached cautiously, he remarked that he was watching two hornpouts *(Ameiurus)* swimming about in a school of polywogs." Charles adds, "I showed him his 'polywogs' were young hornpouts," and explained the breeding habits of this species (a catfish). Although Bacon, who was the man, was shown to have made an erroneous observation, he and Charles became and remained good friends and frequent collaborators in the study and identification of "a difficult moss, a puzzling carex, the call of a night bird or an intricate crossword puzzle." Finding the answer was Bacon's one all-absorbing goal. Moreover, he was like Rafinesque (a distinguished taxonomist) in his broad interests and untiring energy, yet without a trace of a desire to assign names or receive credit. Charles writes, "I learned much from his intense objectivity, quite unhampered by a highly imaginative and poetic side of his nature."

Only a few days after finding a collaborator Charles showed him "a bird's nest containing a foreign egg which I suspected was that of a cuckoo." Walter Bacon identified the owners of the nest as indigo buntings. Together they visited the taxidermy shop of J. Waldo Nash, who had an egg collection, and decided the foreign egg "was indeed that of a cuckoo (a very unusual find)." On the same day Charles learned for the first time of several books on birds available in the public library of Norway. On that same day, therefore, he was introduced to two stimulating naturalists as well as to the works of Baird, Coues, Maynard, and Chapman. From these it was but a short step to Asa Gray's *Manual of Botany,* Jordan's *Manual of Vertebrates,* and other volumes which he soon owned. Charles writes: "Before long, I was aspiring to know, at least by name, all living things about me. It was easy to learn the Latin names of new species as I identified them, and I caught up on old acquaintances by getting a few names in mind each morning and noon and rehearsing them while I worked." Charles had acquired one of the distinctive qualities of a naturalist—the knowledge of plants and animals by their Latin names.

At about this time his grandmother Haskell, not to be outdone by all this learning from nature, decided to give "us children" another demonstration of how things were done in earlier days—this time on how cheese was made and on how to cut a forked stick on which to dry a calf's stomach from which rennet was to be obtained and used in the curdling of milk.

Influences outside of high school continued to affect his way of life and thought. The most influential of these were contacts with citizens prominent in Norway affairs, among whom were George Howe and George Noyes, two members of old Norway families, each about forty years of age. Howe, a graduate of Tufts College, was a well-known naturalist and philosopher, and Noyes was a naturalist, artist, and wit. Charles had for a long time wanted to know them but, "with an ineptitude which has always been rather characteristic," he failed to meet either one of them personally until a special event opened the way.

Having written an article in defense of hawks and owls, he submitted the manuscript to the Norway *Advertiser,* the local newspaper, and then went to call on Mr. Howe, "ostensibly to ask about the approved pronunciation of scientific terms." How excited Charles must have been; Howe "invited me to his rooms where I was amazed at the beauty and wealth of his collections, especially his minerals and insects."

Thus what may be regarded as a naturalist club in miniature had its beginning for Charles. George Howe, who during the day worked sporadically in his father's insurance office or took long walks, at night held forth in his study, which was a mecca for nature lovers and visitors of many sorts. Noyes, the naturalist, was almost invariably there and before long Charles became a regular visitor himself. The group that met in evenings with Howe and Noyes were all familiar with the surrounding country and with much of its animal and plant life. Charles emphasized that they, as did his close friend V. Akers, knew its mineral and artistic resources better than he. All of them regarded Thoreau as a kind of intellectual patron inasmuch as he used "our language and had much the same outlook and humor." "In these respects Emerson on the whole fell a little short." "This was in the days before Thoreau had been 'rediscovered' and when popular nature study was in its infancy." The discussions were so lively and stimulating that Charles returned home "rather guiltily along the silent street" on many a winter evening "as late as 9:30 or even 10 o'clock."

The number of naturalists in Norway and its environs was most unusual for a small country town of about 2000 people. At the age of about thirteen years Charles knew personally as many as six able and knowledgeable amateur naturalists. Moreover, Charles adds to the list the names of his father and grandfather in these words: "Without any special technical training he [his father] was a keen observer and had many of the instincts of a field naturalist as, apparently, had his own father."

Thus the large number of devoted naturalists had the effect of producing an intellectual climate highly colored with a strong interest in things of nature. Charles had no other course to follow than to be a naturalist.

Just when he first acquired the idea of becoming a naturalist, however, is uncertain—possibly during the early days on the old farm. A relevant incident cited by Charles has a bearing on this matter. In looking at pet snakes he kept in a barrel, two adult cousins exclaimed, "I guess he is going to be a naturalist." "That was in fact just what I would be," Charles thought. Then he writes, ". . . throughout my whole life I never seriously entertained any other thought."

Somewhat frequently the evening discussions in the Howe study dwelt on matters more or less philosophical. Those of an agnostic or frankly atheistic tenor at first distressed Charles greatly. During his boyhood he had been active "in a kind of diffident way" in church and had "taken the Universalist religion for granted, despite an accumulating volume of complexities." With this religious background his first impulse was to do some "missionary" work against the view of agnosticism. His own thinking had in a manner conditioned him so much that conversion to agnosticism became, in his words, "inevitable but not easy." He wrote, "In due time I acknowledged to myself the absence of proof for the things I had believed and recognized an attitude of agnosticism as probably the only tenable one." The transition involved many restless nights of despair and groping. But in due time "a scarcely less harrowing ordeal was the attempt to build something satisfying and dependable to replace the religion I had lost." After struggles day and night with relative intangibles until a satisfactory and workable basis could be achieved, he finally came to hold the belief that "absolute finality is not an attainable goal and oriented my thinking accordingly—in the end, the new approach offered a better basis for 'serenity' than I had previously experienced."

A few years later at college he observed with satisfaction, "I was amazed at the number of students who were thrown into mental turmoil by aspects of philosophy which then left me quite undisturbed." Also, although he had never read them before, "Descartes and Kant were to appear almost as old friends and fellow seekers for the same goal." He adds, "Nevertheless 'philosophy' (except as I built up my own!) always seems to me particularly sterile, and so did formal logic."

Less than a week before he graduated from high school his mother died quite suddenly on Memorial Day. Almost within the hour of her death she had asked Charles to rehearse his graduation essay. Later that morning he "went up on the hill and looking across acres of blooming rhodora in the valley below recalled a couplet from one of Emerson's poems which she had often quoted.

> If eyes were made for seeing
> Then beauty is its own excuse for being.

The rhodora became a recurring symbol of enduring love for his mother and for nature. (*Rhodora canadensis,* a shrub related to rhododendron, has delicate pink flowers produced before or with the leaves in the spring. It is characteristic of the New England countryside.)

A NATURALIST PREPARES FOR COLLEGE

At the time of graduation from high school in the spring of 1903 Charles had "no expectation whatever of going to college." For nearly two years prior to graduation he had many protracted arguments with his parents on the subject. Contrary to the wishes of his parents he reached the decision that "going to college would be a useless, expensive and disturbing interruption of the simple life I had chosen to live."

As a consequence, Charles remained at home (at the Haskell house on Main Street) "leading a life that must have appeared most unpromising." He continued to participate in routine work of the farm and garden. His free time was spent in the field observing nature and in reading books both "stimulating and broadening." These included *The Descent of Man* by Darwin, *Cosmic Philosophy* by John Fiske, and *Riddle of the Universe* by Haeckel, as well as many controversial books and articles of the late nineteenth century. Once again his grandmother Haskell took an interest in him, this time in broadening his social life by giving him money for dancing lessons. To her annoyance he purchased among other things a copy of Preston's *Theory of Light.* The avowed reason for the purchase was to be able to honor a request to serve as physicist in the organization by George Howe of the local science forum. "I tried to do so, but with no great enthusiasm."

During the year after graduation, which he characterized as "Transitional Year 1903–1904," Charles wrote a diary or autobiographical sketch of "my first twenty years," which unfortunately was lost. In the sketch written when he was sixty-five, however, Charles saw himself "in a clearer light now [1948] than I could then [1904]." His self-analysis is set forth below in his own words.

"From my earliest days, I have been to a degree unsocial. I have not disliked people, but have always felt a kind of social inadequacy, on the one hand, and a personal self-sufficiency, on the other, that has made it easy to be alone. I enjoyed friends, games of strength and skill, but for an all-day trip in the summer or a snowshoe hike in the woods on a cold winter night I preferred to be alone. Because of some notion that 'nature' represented the highest state of perfection, man the enemy of nature seemed of all animals least interesting. I enjoyed music but was never able to carry a tune (a definite hereditary deficiency), and I never learned to dance. Failure to cultivate some of the social graces was in part genuinely due to a greater interest in other things and in part, no doubt, to rationalization of my inherent deficiencies. By the time I finished high school (the lineal descendant of the Norway Liberal Institute) I was far better acquainted with the local fauna and flora than most boys of my age but in comparison with Verrill, and perhaps Whitman, at a comparable age and graduating from the same school, I was woefully deficient. But for all that, and in spite of despairing of ever having a memory such as Professor Smith's, I still planned to be in effect a naturalist, though probably not a professional one. My attitude toward nature was somewhat reflective and at this time I though it not impossible that ultimately I might arrive at some important generalization, even as Darwin had done."

Of this year Charles wrote, "This was one of the best years of my life." In the spring of that year he decided to try at least one year of college and "drew up columns of pros and cons for Yale (Smith and Verrill), Harvard (Shaler, whom I had never met) and Tufts (fewer entrance requirements and less expensive)." The balance finally fell in favor of Tufts College, to which he went secretly in June for entrance examinations and entered in September 1904 as a freshman. Upon leaving Norway that autumn, he wrote in his notebook "with prophetic insight, a warning not to drift thoughtlessly into conventional ways of life. As it happened, I did just that, and then drifted on to baccalaureate and advanced degrees."

A NATURALIST AT COLLEGE

When Charles entered college he was nearly two years older than the average freshman student and accordingly thought of himself as much more "adult" than many classmates and in other respects "intellectually younger than most of them." From the very first he made fairly rigid rules not to study after ten o'clock at night and to set aside some time each week for a trip into the country, to such places as Lexington, Concord, and Walden ("not yet made a resort"); more especially to nearby Middlesex Falls and Mystic Lakes, where "I sought eagerly for *Potamogeton mysticus*," a plant of the pondweed family. The many species of this family commonly have floating leaves that often differ greatly in shape from the submerged leaves. Moreover, the floating leaf is borne on a stalk that permits the leaf blade to rise and fall with the level of the water. In addition, the leaf is waterproofed on its exposed surface. Apparently he had previously concentrated on other families of aquatic plants, such as the water plantains (the *Alismacea*) and the water nymphs (the *Naiadaceae*) and was eager to see a potamogeton in its natural habitat. There is an illustration of a mind that was able to discern fine structural differences of significance among plants and among organisms in general.

Of broader appeal was the rural village of Concord and nearby Walden Pond, a region that boasted an unusual concentration of distinguished original thinkers—poets, philosophers, and/or naturalists. Charles had long been familiar—ever since as a boy of high school age he became a member of Howe's naturalist club—with *Nature,* a book by Ralph Waldo Emerson, and *Walden; or, Life in the Woods* by Henry D. Thoreau. Both books aroused sympathetic feelings in Charles. However, of the two authors, Thoreau the naturalist was more fully understood and appreciated by Charles the naturalist. To both Charles and Thoreau, intimacy with nature was vital and supreme.

Most of the courses in the humanities and arts at Tufts were found to be of interest by Charles. Of one subject after another he thought that, if it were not for biology, this or that subject would be a fascinating one to follow. At this time, which was a romantic period with such authors as Keats looming large, and under the influence of his professors of English and fine arts and of his classmate and closest friend, Clinton J. Masseck, Charles was deeply impressionable—so much so that "I wrote a little." It must have been more than a little since in his third year he was made associate editor of the college literary magazine. Later he was elected to Phi Beta Kappa—"a complete surprise, the more so since I had some poor grades in both German and trigonometry."

His formal training in biology consisted on the whole of pretty much the orthodox morphology of the late nineteenth and early twentieth centuries. The main subjects included comparative anatomy of vertebrates and plant morphology, the former taught by J. S. Kingsley, the well-known comparative anatomist, and the latter by F. D. Lambert, the botanist. Supplemental training included laboratory instruction in elementary biology and participation in a seminar on "Mendelism" by which he acquired a general point of view and an interest in the "genetic basis for racial differentiation." Because of the proximity of the Harvard University campus, he was able to listen to lectures by Professor William E. Castle, the geneticist, and other distinguished scientists and to attend meetings of seminars and the Biology Club. He became a member of the New England Botanical Club and frequently attended meetings of the Boston Society of Natural History.

With a natural bent for the theoretical and having been previously influenced by Darwin and Louis Agassiz, Danforth was prepared to seek knowledge of the processes by which life develops from an egg and thus gain an understanding of nature in general. With this objective in mind, early in his freshman year he sought permission to obtain eggs for a study of chick embryology. Instead of having this request honored he received an assignment to work on pteropods (wing-footed snails) which Dr. Kingsley had collected, fixed, and preserved in alcohol at South Harpswell, Maine. With "much supervision" the results of this study were published in 1907 under the title "A new pteropod from New England" (with four plates of his own drawings). By way of contrast he published in his senior year (1908) an article on numerical variation in a daisy, of which he was justly proud.

WASHINGTON UNIVERSITY, 1908–1922

The summer after graduation from Tufts was characterized by a series of dramatic changes that led step by step to a professorial career of distinction in biological research. Early that summer he fully expected to return in the fall to his alma mater on a fellowship. Moreover, he was at work on the morphology of the head of the 20-mm embryo of the catfish *(Ameiurus)*, a study that began in 1907 at Dr. Kingsley's suggestion and that had continued during his senior year. (It may be noted here that nothing came of this work until later, when it served as the dissertation for the master of arts degree awarded to him in 1910 by Tufts College.) Then, quite suddenly Danforth received from Professor R. J. Terry an offer of an instructorship in the Department of Anatomy at Washington University Medical School in St. Louis at a salary of $800 a year.

The decision was an important, yet a very difficult, one to make. Danforth pondered long and hard. In going to Washington University, he reasoned, "I could make substantial payments on my indebtedness [to his father] and still have my summers free of the necessity of earning money." Moreover, "this fortunate situation" would permit him to spend a number of successive seasons at the Harpswell Laboratory on the seacoast of Maine, which was chiefly a Tufts enterprise under the direction of Dr. Kingsley. There was an added inducement: He "could continue to work on fish," as Terry promised in the offer.

The advantages seemed to outweigh any disadvantages (none mentioned), and he decided to accept the offer. In making this decision "I automatically gave up the idea I had been toying with during the summer of going into botany rather than zoology."

In September 1908 Danforth arrived at St. Louis in the mood of a pioneer in the far west, that is, one venturing beyond the Allegheny Mountains. The romantic old city of St. Louis opened up new vistas to him. Moreover, the countryside, the people, and their activities "all differed appreciably from those to which I had been accustomed" in New England, especially in Norway and in the metropolitan environment of Boston. Professor Terry, a doctor of medicine, a native and long-time resident of St. Louis, took a special interest in the newly acquired naturalist on his staff. He gave generously of his time in introducing Danforth to historic restaurants and other old places in the city, and to caves and cliffs and Indian mounds. Danforth commented, "Medicine seemed to be the best field in which Terry could cultivate his interest as a naturalist." On Sundays, as had been his custom of old, Danforth usually explored alone in the many outlying regions of the countryside. However, there was a difference from earlier explorations in that little or no comment on plants or animals was made in his autobiographical sketch.

He soon began, at Terry's suggestion, the study of Polyodon, commonly known as paddlefish, a fish peculiar to the Mississippi River. His interest in a habitat study of Polyodon took Danforth to the lakes and muddy streams in the bottomlands of the Missouri and Illinois rivers, branches of the big Mississippi. By 1912, these explorations had been extended to Reelfoot Lake (Tennessee) in search of the elusive eggs and young of Polyodon.

As time moved on he became a member and secretary of a "flourishing biological club" in St. Louis, composed of naturalists and medical men. He was likewise a member and secretary of the St. Louis Academy of Sciences. Further, he was occasionally invited to the meetings of the distinguished

"Twelve Apostles," a group comprising an ornithologist, an archaeologist, a herpetologist, and nine other scientists. The fine personalities in these organizations led Danforth to have "a sincere respect for the amateur naturalists of St. Louis, among whom there was a mellow atmosphere of goodwill that seems to have been largely lost in these harsher times" (written in 1948). The foregoing lines again show evidence of Danforth's joy in being a naturalist and being among men of similar interests.

In the Department of Anatomy he was both an instructor and a student for a doctoral degree. His immediate superior, Victor E. Emmel (later Professor of Anatomy, University of Illinois), and Danforth had the joint responsibility of organizing and developing courses in embryology, histology, and neurology. The available study material for these courses was meager, so it was necessary to work many evenings at the old laboratory at Eighteenth and Locust to keep ahead of the students. Danforth's "necessary association with recently dead bodies" was so repugnant to him that it took time before he "could think of no better final dissolution than being dissected by two eager medical students."

The question of a doctoral degree naturally arose soon after he entered the university. It seemed desirable to prepare for either an M.D. or a Ph.D. degree, or the combination, as Dr. Terry urged. Danforth reasoned that while his attitude toward "man" had undergone great changes since his pre-college days, he still would have preferred farming to the practice of medicine. So he decided to take the Ph.D. degree, with the inclusion, however, of self-imposed provisions for attaining a breadth of knowledge of other disciplines in the medical curriculum. This enabled him to be "on the inside of medical education." His major subject was anatomy; his dissertation was on the anatomy of Polyodon, a fish of unusual interest in the evolution of teleosts. His minor subjects included human physiology and special investigations in animal and plant physiology. He was awarded the Ph.D. degree in 1912 by Washington University.

It seemed quite natural that Danforth, having a good understanding of the general genetics of animals and plants and having the anatomy of man as the main subject of his study, should take an interest in human heredity. Somehow his view of man had changed from what it was in 1903–1904 (see p. 15). To this end in the summer of 1913 he went to Cold Spring Harbor where he took a course in eugenics given by Charles B. Davenport and H. H. Laughlin. He also became acquainted with the work of the Eugenics Record Office, an institution then devoted to the study of human heredity, factors of race betterment, and improvement of the inborn traits of the race. Thereupon he became active in the study of human heredity, as his record of publication shows, and offered a course in heredity for medical students. More perhaps than in any other field of biology he obtained the highest recognition for his original contributions in general and developmental genetics.

That summer the most beautiful of all events in his life took place. Riding on the bus from the railroad station to the laboratory at Cold Spring Harbor, Danforth noticed a young woman who was also obviously making the trip for the first time. It so happened that Danforth was assigned to the same table as she in the dining room. She was Florence Wenonah Garrison, a teacher of science in a high school of Wilkes-Barre, Pennsylvania, who had come to the laboratory for further work in biology. They soon took boat rides together across the moonlit harbor and enjoyed corn roasts on the old Sand Spit; as with many another couple having mutual biological interests, a romantic association developed. Charles and Florence were married on June 24, 1914, exactly one year after their first meeting. Most naturally they went to an oasis of gentle wilderness in the Maine woods for their honeymoon.

In the fall of 1914, when it became apparent that the United

States would be drawn into World War I, Danforth joined with many others and applied for assignment to an officers' training camp. Although in due time he received instructions to report, he was kept at the medical school to continue teaching medical students. What could an anatomist do to further the war effort? Through a questionnaire he became impressed with possibilities in the field of physical anthropology. Thus began an interest that brought him into local and national organizations. He subscribed to the very first volume of the *American Journal of Physical Anthropology,* founded in 1918 by Ales Hrdlicka, and later served on the editorial board of that journal. He was one of the charter members who helped organize the American Association of Physical Anthropologists. He subscribed to *Genetics* "in advance to help insure launching of the project" proposed by George H. Shull.

It was not until the summer of 1919 while Danforth was at Cold Spring Harbor with his family (wife and two small children) that Dr. Charles B. Davenport persuaded him to participate in an anthropometric study of demobilized soldiers. Leaving his family at Cold Spring Harbor he went to Washington, consulted Dr. Hrdlicka on plans for several camps, and then went to Camp Dix where he took charge of the anthropometric work, leaving in time to return to teaching in the autumn.*

In the summer of 1917 he taught a course in ornithology at the Biology Laboratory of the University of Montana at Yellow Bay on Flathead Lake. The summers of 1920 and 1921 were spent at the Marine Biological Laboratory at Woods Hole, where he worked on the problem of human populations, a subject that had interested him for many years. The resulting article turned out to be "my best mathematical effort" (for appraisal, see p. 32). Toward the end of each summer he and

* For comment on frequency of syndactyly in soldiers stationed at Camp Dix, see *Eugenics, Genetics and the Family,* Vol. 1. (Baltimore, Williams & Wilkins Company, 1923), p. 121.

his family returned to the Norway country that he loved so much as a boy.

Sometime during the year 1921 he was invited by Dr. A. W. Meyer to join the staff of the Department of Anatomy of Stanford University. After fourteen years on the faculty at Washington University, the decision to leave was not an easy one. It meant interrupting several research projects well under way, one of which was a study of hypertrichosis in the human (which he entered into reluctantly with a surgeon through whom a research fund had been provided). This study was left for Danforth's doctoral student and research assistant, Mildred Trotter. To break a close association with a colleague, Edgar Allen, the discoverer of the ovarian follicular hormone, was disheartening. Danforth tells of aiding and encouraging Allen in his very first success in producing estrus in a spayed mouse. Despite the multitude of ties in St. Louis, "we embarked cheerfully on the new venture."

STANFORD UNIVERSITY, 1922–1969

Except for a period of fourteen years at Washington University, Danforth's professional life was connected with Stanford University. In the fall of 1922 he entered Stanford as an Associate Professor of Anatomy and was promoted to full professorship in 1923. Fifteen years later (1938), upon the retirement of Arthur W. Meyer, Danforth succeeded him as executive head of the Department of Anatomy, a position he held until his retirement in 1949, a span of eleven years. After official retirement he remained active in research for many years, as the list of his publications testifies.

In entering upon his duties at Stanford he was impressed by Dr. Meyer's forceful approach to the teaching of gross anatomy, which, owing to Meyer's emphasis on functional and pathological aspects, was made "interesting and stimulating." To Danforth the ideal combination would be the Meyer approach and an interpretation of human anatomy in terms of the evolution of organ systems, a field in which he had extensive training. On this matter Danforth wrote in 1948: "I have never been willing to concede that anatomy should be regarded as other than an absorbing subject in its own right, by no means a mere stepping stone. I consider it almost axiomatic that an interest in normal structure and function should be characteristic in any branch of medicine, and that has been the real, if not always expressed, attitude of most of the outstanding clinicians with whom I have come in contact."

Most of his teaching of gross anatomy was highly personal, conducted through conversation with individuals or small groups of students in the laboratory. With a breadth of knowledge, enthusiasm, and patience Danforth was able to kindle interest among medical students in learning anatomy. As one student put it, "He made the dullest things alive." In a similar way he encouraged the faltering student.

His scholarly interests in the heredity of man and the human body and its parts, which, as noted above, reached a turning point in 1913, continued to dominate his thinking and teaching. The course on human heredity, which he first organized and gave to medical students in 1914 at Washington University, was offered each year from 1926 to his retirement at Stanford. The course dealt with the facts and problems of heredity in relation to the individual and the population as a whole. He also offered a course on physical anthropology, in which the lectures laid emphasis on anatomical variation and heredity in man. His lectures have been characterized as showing comprehensive knowledge of the subject matter as well as a depth of understanding. The search for "true knowledge" was a characteristic of them.

As executive head of the Department of Anatomy, Danforth was capable of winning and holding the trust of his faculty colleagues in the department. Without seeming to do so, he administered in a quiet and patient way. Moreover, he had the steadiness of purpose to serve as a focusing center of group enthusiasm by arousing enthusiasm for research and teaching among staff members and students. Occasionally he was privately nettled by discourtesies or by any attempt to take advantage of his generosity. He could suffer in silence.

With respect to university affairs at large he soon found the atmosphere of the campus, with its large number of departments representing a wide variety of disciplines, very agreeable and intellectually stimulating. However, inasmuch as the clinical departments were not established on the campus until later, he missed the everyday contact with clinicians and their problems that he had had at the medical school of Washington University. At Stanford he entered more fully into university life through the years, serving on a multitude of committees and as president of Phi Beta Kappa; he was a member of a research club and others of a like nature. He had adopted Stanford as his own.

In addition to his professional activities on campus he was a member of and often participated in both state and national professional societies. The number of them is legion. Among them are the American Philosophical Society, American Eugenics Society, American Society of Naturalists (president, 1941–1943), American Society of Zoologists, California Academy of Sciences, California Academy of Medicine, Genetics Society of America, Society for Developmental Biology, and Society for the Study of Evolution. In 1942 Charles Haskell Danforth was elected to the National Academy of Sciences.

SCIENTIFIC WORK—AN APPRAISAL

Among the first publications by Danforth were those concerned with the morphology of a marine snail (a study of a new species) and the comparative anatomy of Polyodon. These papers represented fields that fitted in with his teacher's research specialty. The articles on Polyodon listed in the bibliography satisfied the thesis requirement for the Ph.D. degree awarded by Washington University. Together they present a thorough and detailed knowledge of the anatomy of an ancestral fish, then commonly known as a ganoid fish and now regarded as an aberrant chondrostean survivor. The work on Polyodon served to strengthen his qualifications as an anatomist. There were, however, fields of even greater interest to him and more in keeping with his talent as a naturalist.

Three of these early publications deal with questions of variation and speciation; they represent ideas that probably came to him in reading Darwin at twelve years of age. The first of these papers, published in 1908 while he was a senior in college, dealt with the number of florets (tiny flowers) in the flower head of the common daisy, a composite plant. By comparing the number of ray florets of plants from three different geographical regions, Danforth was able to show a relation between mode (number of ray florets) and the external environment. The paper represents, as he stated in 1948, "my natural 'approach' as anything I have written quite independently." Another observation made at about the same age was on the occurrence of a color variation in two forms of plants of the same species of the foam flower. In using the term "dimorphism" in the title he remained noncommittal as to the cause of the variability. Yet he anticipated a Mendelian interpretation by noting that the two forms of plants occurred together in all places in which he found the species and that they might be useful in "cytological and Mendelian" analysis.

In 1909–1910, while he was studying for the doctoral degree, Danforth's curiosity was aroused over the question of factors controlling periodicity in the appearance of reproduction phases in many algae. Although algal periodicity was a matter of common observation, there was little experimental evidence on whether it was due to an inherent tendency or was environmentally induced. On this question W. Benecke had postulated, on the basis of his work on growing *Spirogyra communis* in different media, that the loss of ammonium salts—removed from water by the growth of angiosperms—would induce conjugation under natural conditions. Danforth wondered whether the absence of ammonium salts could be taken as a specific stimulus. He repeated the experiments of Benecke, using other species, five different ones of *Spirogyra*. Danforth obtained results showing specific differences in the reaction of filaments and zygospores in the five species. Indeed, it is possible that *Spirogyra* "is inherently periodic in its functions, although its periodicity may be extensively influenced by its environment."

Very soon Danforth turned away from problems of variation and speciation in plants—never to return to them—to the field of human heredity, a field in which he was to excel as a contributor of new knowledge. As an anatomist and a teacher of anatomy, Danforth intuitively felt morally obligated to include man among his own investigations. To him almost any structural variation from the normal became a problem for exploration. It became just as natural for him to study any anatomical variation in the human body as it was to study variation in the number of ray florets in a common daisy. The human body became for him a part of nature about the time (1912) he acquired the Ph.D. in anatomy. In the summer of the next year he studied eugenics, which in part led him to formulate a program of study of anatomical variations from the standpoint of genetics, not only of man but likewise of birds and mammals. Progress was rapid. In one year (1914) his first paper on a dominant mutation for cataract was published, and by 1921 he had publised articles on a variety of hereditary traits or mutations in man. Among these are such significant ones as (*a*) suppression of the palmaris longus muscle, apparently a dominant trait, and (*b*) the complete absence of hair from the middle segments of the digits, a recessive trait (see p. 49).

As Danforth customarily worked on a variety of problems at the same time, he early saw the suitability of studying family histories of man in which pairs of twins occur, in order to elucidate the hereditary tendency for twin production, and also in order to investigate the degree of resemblance between members of a pair of twins, particularly where the sex is the same.

Two classes of twins have long been recognized, monozygotic twins and dizygotic twins. It has been commonly assumed that twins of opposite sex are necessarily dizygotic while those of the same sex may belong in either class. Dizygotic twins may sometimes resemble each other closely and monozygotic twins may be quite different. Moreover, absolute identity is never attained. How may these classes be distinguished? Is the relation of the fetal membranes (amnion and chorion) in which the twins develop a reliable criterion for the recognition of monozygotic or dizygotic origin of twin pairs?

If a pair of twins of the same sex at birth is enclosed in a single set of membranes, they have arisen from a single ovum. However, when surrounded by separate sets of membranes, they are not necessarily dizygotic. By reasoning from a study of Simon Newcomb's data of 37,621 pairs of twins (born in Germany and France), Danforth in 1916 pointed out that 29+ percent of all twin cases are monozygotic, whereas the number of monozygotic twins given in textbooks of obstetrics is about 15 percent when based on the relations of fetal membranes. The difference between 15 percent and 29+ percent represents the number of cases in which monozygotic twins develop in separate sets of fetal membranes. Here is a discrepancy that was generally overlooked. Thus, by number of twins and reasoning, Danforth deduced that fetal membranes in which twins develop have only a limited value in the diagnosis of their zygotic origin. Danforth was "the first to use the similarity diagnosis [phenotypes of twins] as a check of the diagnosis based on the afterbirth [number of placentas and chorions]." *

In a study of resemblance and difference in twins Danforth

* See Curt Stern, *Principles of Human Genetics*, 3d ed. (San Francisco, W. H. Freeman & Company, 1973), p. 642.

(1919) asked why there are differences in twins known or assumed to be monozygotic. Why are such twins not actually identical? In seeking an explanation of the differences Danforth argued that since each member of a twin pair represents but one half of a single zygote, there is little reason to expect them to resemble each other more closely than do the two lateral halves of a single individual. Moreover, the two sides of the same single individual are by no means identical; for example, right and left sides of the face are rather frequently asymmetrical. Whatever may be the cause of variation between the two sides of the body when they develop as a single individual, it is reasonable to expect that they will be equally effective when each half of the primary formative cell-mass develops as a separate individual. It might therefore be predicted that monozygotic twins would differ from each other in the same respects and to the same degree as two sides of the body differ in ordinary individuals.

The theoretical considerations discussed by Danforth serve to account for most of the resemblances and differences actually observed among twins; also they aid in understanding why monozygotic twins are not absolutely identical and why dizygotic twins are very often closely similar. Such features "seem to be due more to the inherent constitution of the germ plasm than to influence of the environment."

Thus, Danforth has brought to the forefront a problem of supracellular organization, namely, that of the nature and developmental origin of asymmetry. It is well known to anatomists that man and many other vertebrates are inherently bilaterally asymmetrical and not strictly bilaterally symmetrical as is popularly thought. Furthermore, asymmetrical organization manifests itself in the fertilized egg and/or the embryonic cell-mass from which two growth centers arise, each developing into a distinct individual. Twins derived from a single zygote may be thought of as parts of a single system of asymmetrical organization, each half of which upon separation undergoes a reorganization, that is, a reordering of symmetry pattern of cells. Each half is a germ whose developmental history is peculiar to it. By such a view one may account for mirror-image duplicates of hair whorls and other dissimilar features in like twins.

Danforth also carried out an analytical study of structural anomalies of the foot of the common domestic fowl in which he was concerned with the kinds of factors that have a "determining influence" on the ontogeny of brachydactyly. He presented evidence (1919) on the bases of breeding tests and correlations in developmental morphology that brachydactyly (shortening of digit IV), syndactyly (formation of two digits from digit number I), and ptilopody (feathers on the tarsus and toes of the foot) constitute an "heredity complex," that is, they are primarily associated in heredity and are primarily caused by a single gene.

The foregoing seven years of pioneer explorations may be characterized as a period of intensive study of mutations in man as well as in the common fowl. The record when scrutinized shows that he had acquired an excellent command of the literature on the phenomena of mutation and theory—including the relevant works of H. S. Jennings, Sewall Wright, Kristine Bonnevie, and others. As his factual knowledge and his understanding increased, his thoughts and ideas tended to focus on the question of mutation frequency in the human population. He was thus admirably well prepared for a quantitative study of mutation frequencies, as will immediately become apparent.

From about the year 1913 onward, Danforth (as noted above) eagerly participated in promoting the science of human heredity and the study of eugenics during their early history. It was a natural bent for Danforth to feel he "ought to do something" for the oncoming Second International Congress of Eugenics to be held in New York City on September 22–28, 1921. He worked at Woods Hole much of the summer of 1921 in preparing a manuscript entitled "The Frequency of Mutation and the Incidence of Hereditary Traits in Man." This was a result of his thought on the problem of human population genetics, in which he had been interested for many years.

This paper is a highly original attempt to determine the mutation rates of dominant human genes under the assumption of a steady equilibrium in large populations between the effects of recurrent mutation and adverse selection. Such an equilibrium is to be expected because mutation, recurring at a given rate, tends to increase the frequency of the gene in question in proportion to the frequency of its normal allele and thus practically uniformly as long as it is rare, while selection tends to reduce its frequency in proportion to its own frequency. There must be a certain frequency at which these processes balance. Danforth noted that the number of generations through which an individual mutant gene persists in the population is the reciprocal of its selective disadvantage. His estimate for the mutation rate per generation of a particular gene was thus the ratio of its estimated equilibrium frequency to its average persistence (in generations).

From a study of pedigrees, he estimated the average persistence for the dominant traits polydactyly and syndactyly to be about three generations in both cases. The estimated gene frequency being about one in two thousand in both, his estimates for the mutation rates were both about one in six thousand. He noted, however, the likelihood that this estimate of persistence from pedigrees was less than the actual persistence, so that the true mutation rates might be considerably less than one in six thousand.

This pioneer contribution was overlooked for many years. As noted by L. C. Dunn in his *Short History of Genetics* (1965), this method of estimation of mutation rates for dominants, given in Danforth's address in 1921 and published in 1923, preceded use of the same idea by J. B. S. Haldane and by L. S. Penrose by fourteen years. Moreover, none of those who later used it attributed its origin to Danforth. In a similar vein, Curt Stern comments: "His pioneering paper remained without consequences and the same method had to be reinvented in 1935 by Haldane and by Penrose (see Gunther and Penrose)." *

In 1950, however, H. J. Muller, who had listened to Danforth's address at the 1921 Congress of Eugenics, called attention to Danforth's pioneering role and used his principle extensively in developing his concept of "genetic load" with special reference to man.

The long period of neglect poses a question as to the reason. At my request, Sewall Wright has commented as follows:

"Danforth's address in 1921 and publication in 1923 probably did not attract much attention at the time because few geneticists were then actively interested in the subject. Its fate was that of many pioneering papers which are not actively followed up by their authors. The few who were interested probably took equilibrium in itself for granted since it is merely the negative aspects of the principle of natural selection as applied to gene mutation: The rare favorable mutations tend to become established, while the unfavorable ones tend to be held at low levels of frequency. With respect to Danforth's particular formula, they probably questioned whether the average number of generations of persistence of a mutation could be determined sufficiently accurately for valid estimates.

"Most pedigrees involve only a few generations because of lack of knoweldge about remote ancestors. Thus the estimated average number of generations found in pedigrees is unlikely to exceed three by much, even though the real average is more than a hundred. Moreover, many dominant traits of which polydactyly is a notable example, show incomplete penetrance and thus manifestation often skips one or more generations. Another complication is that the same condition may arise from mutations at more than one locus.

* Curt Stern, *Genetic Mosaics and Other Essays* (Cambridge, Mass., Harvard University Press, 1968), pp. 3, 7.

"Haldane [*Proc. Camb. Phil. Soc.,* 23 (1927):838–44] was the next author to give quantitative expression to the idea of equilibrium. According to his formula, the mutation rate for a gene is the product of its equilibrium frequency and its selective disadvantage, which in principle requires merely comparison of the reproductive successes of affected individuals and their normal siblings. Haldane, however, used it merely as an aspect of his theory of evolutionary dynamics on which he wrote a series of papers between 1924 and 1934, including a book (1930) which attracted much interest.

"As noted, it was not until 1935 that new estimates of human mutation rates were made by Haldane himself and by Gunther and Penrose. These estimates (2×10^{-5} for sex-linked hemophilia, 10^{-5} for dominant epiloia) were more than an order of magnitude smaller than Danforth's estimate for polydactyly and syndactyly.

"Whatever the difficulties in using his particular formula, Danforth's paper should clearly be credited with being the first to point out the possibility of using the principle of equilibrium in calculating human mutation rates."

His work on the frequency of mutation in man was only one phase of a broader program of investigations. In fact, he was simultaneously at work on a miscellany of specific problems that apparently were of even greater interest and appeal to his fertile mind. The problems had a common objective, that of investigating the role of genes in the ontogenetic processes of structural mutations. From the very first he was concerned with the kind of factors that play a role in the developmental anatomy of brachydactyly, polydactyly, and the like in the domestic fowl and later with their role in the production of polydactyly in the domestic cat.

Polydactyly, when considered as a "genetic and morphological entity," provides excellent material for the analysis of the role of the genes and other factors in the morphogenesis of supernumerary digits of the foot, that is, in the matter of extra toe production. By a long-range research program comprised of breeding tests and an extensive study of the embryology and morphology of the normal and polydactylous foot, Danforth discovered that polydactyly in the cat is a trait controlled by a single dominant gene.

Moreover, he suggests that the chief effect of the gene is to "incite" an excess of digit-forming tissue in the preaxial part of the limb bud. Indeed, the excess digital tissue may be the only "direct function of the causative gene." At first it is a bulge of unorganized tissue. The excess of unorganized tissue is viewed as disturbing the normal balance of developmental processes in such a way as to change the size and/or number of digital lobes produced. The amount of digitogenic tissue present at a given *critical moment* during the organization of the limb bud material is postulated as determining the grade of polydactyly.

Thus Danforth has brought the subject of polydactylous limb development to the very threshold of contemporary embryological formulation. His idea that excess digital tissue is the direct function of the dominant gene is in consonance with the discovery of E. Zwilling (1956) that a typical polydactylous limb develops from the combination of mutant mesoderm and normal ectoderm in chick embryos. Mutant mesoderm appears to be the equivalent of Danforth's "digital tissue" [mesoderm] in that both are endowed with polydactylous potentialities, which, however, can only be realized through interaction with specialized ectoderm.*

* It is now firmly established that limb morphogenesis in the chick embryo is the resultant of reciprocal interactions of an ectodermal thickening (ectodermal ridge) and underlying mesoderm. A similar pattern of ectoderm–mesoderm interactions is characteristic of the limb bud of the mouse in which correlation between structural and/or cytochemical changes in areas of thickened ectoderm and in the underlying mesoderm take place—properties that are maintained to the tip of each digital bud [J. Milaire, in Robert L. DeHaan and Heinrich Ursprung, eds., *Organogenesis* (New York, Henry Holt, 1965)]. Moreover, the limb buds of many mammals are characterized by an area of thickened ectoderm at their tips. Such an ectodermal specialization serves as a marker or clue to the onset of reciprocal interactions with the underlying mesoderm [see O'Rahilly, Gardner, and Gray, *J. Embryol. Exp. Morph.*, 4 (1956):254].

To Danforth "the hair follicle * is a kind of 'biological microcosm' in which almost any problem relating to growth, differentiation, decline and rejuvenescence of tissue can be studied to advantage." The study of such a wide variety of problems was initiated in an auspicious manner. While riding on a streetcar in Wilkes-Barre one summer, Danforth observed, in his words, that "a man in front of me draped his arm over the back of the seat and I noticed that while his arm was very hairy the middle segments of his fingers were free of hair and so, I observed, were my own; but I knew this was not generally true." So far as he was aware, no one before had recognized this variation as possibly hereditary. This was to Danforth a fertile source of inspiration. He at once began an extensive study of hair on the digits of man that showed the presence or absence of hair on the dorsal aspect of the middle phalanx (mid-digital hair) is genetically determined, the presence of hair being dominant. Danforth (1921) was apparently the first to record these conclusions.

Moreover, the functioning of the individual follicles of the human pilary system shows a remarkably high degree of autonomy in the length of successive cycles. Such autonomy is maintained over long periods and is not readily disturbed by external factors. Each follicle has its own individual rhythm which is relatively constant and frequently does not synchronize with the rhythms of neighboring follicles. How are these characteristics and potentialities acquired? Danforth searched for the answer in the developmental arrangement of hair follicles in the neonatal mouse, that is, before hair papillae are visible. The hair papillae were found to arise in an orderly manner in the skin of the back of the mouse, from which Danforth reasoned that the skin at first has a generalized capacity for forming hair papillae (follicles in certain regions of the skin show specializations which suggest a form of embryonic predetermination).

* At the base of the follicle is the hair papilla, which comprises a dermal component covered with epidermal cells from which the hair is generated.

Each papilla during its development creates a negative zone (conceived of as having inhibitory forces) immediately surrounding it. A few papillae would then arise at the intersection of negative zones. Danforth in this speculation touched upon a contemporary view that the embryonic determination of the spatial pattern in the distribution of hair papillae and/or of feather papillae is the resultant of inductive interactions between the dermis (mesoderm) and epidermis (ectoderm) and alignment of forces in the dermal cells and a lattice of collagen fibers.

With his expert knowledge of comparative anatomy and of human heredity, Danforth raised the question of homologies of hair, the "most distinctive characteristic of mammals," the "highest" class of vertebrates. From a thorough analysis of observations bearing on homologies of hair, he was able to present a thought-provoking new theory. Generalizing from the new data, he pointed out that there is no one-to-one correspondence between hairs and any of the structures (e.g., scales of a common reptilian ancestor) from which they are supposed to have been evolved, nor between the hairs of one mammal and those of another. These facts, together with the ontogeny of hair, are interpreted by Danforth (1925) to mean that the number and character of hairs that appear are determined by factors which come into play during development. In general these factors have a hereditary basis. The resemblance between hairs and their supposed homologous structures may be explained on the grounds that several structures owe their development to the action of groups of factors, some of which are in common with those that produce hair. It is in the causal factors themselves that the real basis of homology is to be sought. Homology between hair and a related structure is dependent upon the similarity of genetic factors involved in their production. These concepts make it possible to arrive at a more satisfactory meaning of homology of hair in relation to its forerunner structures.

Danforth maintained a deep interest in the biology of human hair and its ramifications over a period of many years, with the result that we now have a broad and secure foundation of developmental morphology and physiology of the hair follicle (1925 and 1939). His synthesis of new and old facts stimulated new ideas and concepts that will serve as a challenge to future investigators interested in questions of determination, differentiation, and functional rhythmicity.

The antecedent of Danforth's extensive work on mice was a leave of absence granted by Washington University in order that he could spend a year (1910–1911) in the anatomy department of Harvard Medical School. Professor C. S. Minot gave him the "job of adding fertilization and segmentation stages of a mammal to the Harvard Embryological Collection." The mouse was chosen, and in carrying out the assignment Danforth gained experience in the breeding of this mammal, which is such a highly suitable animal for the study of heredity. He writes, "The initiation of my work with mice thus dates from 1910." Upon returning to St. Louis, he soon established a colony of mice and organized a full laboratory course in embryology based entirely on mammalian material, probably the first to do so. On research productivity with mice, Danforth facetiously remarked: "Few, I think, have raised more mice and kept more extensive pedigrees in proportion to their published papers."

At the outset Danforth envisaged the value of using mice for the study of mutations under controlled conditions. More specifically, he had in mind a study of the genetic makeup of the anomalous individual and the embryonic development of its structural anomalies. In this way new insights may be gained on the developmental processes and potentialities.

Although he started to build a colony of mice at St. Louis, it was in 1923, one year after his arrival at Stanford University, that he discovered the *first* anomalous specimen from a stock that had been inbred for several generations. Having this anomalous mouse, it was possible to isolate a strain in which about 20 percent of the living young showed some degree of posterior duplication, ranging from typical cases of *duplicitas posterior* to individuals that scarcely deviated from the normal (Danforth, 1925 and 1930). In mice with posterior duplicity may be found four hind legs, two urogenital openings, four kidneys, four gonads, etc.

To Danforth the posterior doubling (double monsters) provided valuable material for a study of the developmental process. There is evidence, he pointed out, of some direct and determining influence of one region upon another, through an impulse exerted directly with an intensity proportional to distance. This was a phenomenon akin to the "organizer effect" of H. Spemann, which is especially evident in the developing limb bud. Danforth fully realized that a more complete picture of the embryology of these posterior doubles is essential before any light can be thrown on morphogenetic processes.

It is clear from the foregoing considerations that Danforth fully recognized the value of posterior duplications and of other abnormal variants in their bearing on the nature of developmental and/or morphogenetic processes. As will be immediately apparent, he did not continue the challenging problems that he initiated.

In October 1936, Danforth, in a most generous act, sent four short-tail mutants (2 ♂ + 2 ♀) of the posterior duplication stock to Professor L. C. Dunn of Columbia University. In January 1938, Dunn and S. Gluecksohn-Schoenheimer (*Genetics,* 23: 146) published an abstract which states: "Short-tailed mice found by Prof. C. H. Danforth among descendants of the posterior duplication stock have been tested and found to contain a new mutant. The short-tailed ones proved to have a new allele with dominant effect on skeleton and some other structures (e.g., kidneys) and a recessive lethal effect shortly before birth. . . . We named it 'Short-Danforth' with symbol *Sd. Sd* homozygotes were found to have no kidneys, no excretory openings, and no vertebrae posterior to the lumbars and this proved to be useful in studying several embryological problems such as the relation between the development of the ureter and the differentiation of the metanephros. Moreover shortness of tail is due to absence of posterior part of the notochord. *Sd* was an important tool in one stage of developmental genetics."

To Danforth, mice and men and birds went "hand in hand" as implements for testing ideas by thoughtful observation or by experimentation. For certain kinds of problems, however, birds were uniquely suitable among vertebrates. They were selected as especially suitable animals for the exploration of what Danforth had in mind, namely, the role of genetic and hormonal factors in the phenotypic characterization of plumage. Sex in birds is commonly reflected in striking plumage differences in feather structure, color, and color pattern, that is, the phenomenon of sexual dimorphism is displayed in plumage.

When in 1922 Danforth arrived in Stanford he brought with him "some bantams." The bantams were bred *inter se* and became the center about which he assembled many diverse breeds of the domestic fowl and of exotic birds ranging from specimens of red and gray jungle fowl to Reeves's pheasants and even to Brewer's blackbirds. At one time, in 1939, the collection gave the writer the impression of an aviary in miniature.

The common domestic fowl, owing to racial differences in feather color and/or color pattern, afforded excellent material for analyzing the interplay of developmental factors in feather differentiation. For such an analysis Danforth used the very simple technique of grafting pieces of skin from one newly hatched chick to another of different breed. The site of interchange of skin pieces between chicks of different breed was the lumbosacral region where sexual dimorphism in the feathers is most clearly expressed. The graft (covered with down feathers) became either permanently incorporated as an integral part of the host or after varying periods of normal growth and activity underwent regression and was lost. Since regression did not occur in autografts, the observed regression was regarded as a consequence of tissue incompatibility—a host vs. graft reaction. (When skin grafts persist, it is now believed that the host has actively acquired tolerance to the foreign graft and hence develops under the influence of its genes.)

Furthermore, the potentialities of the chick skin were already fixed at the time of hatching; that is, the grafted skin and its individual feather germs produce contour feathers (replacing down feathers) not only characteristic of the donor breed but also tract specific (lumbosacral). In some instances feathers (at the edge of the graft) had mosaic patterns comprised of donor and host colors or a barred pattern, as, for example, in a Barred Rock graft on a Rhode Island Red host. These mosaic patterns were correctly interpreted as genetic mosaics. Danforth, however, was somewhat puzzled as to their mode of origin, largely because at the time (1927) little or nothing was known about the migration of pigmentoblasts (melanoblasts). He did recognize the possibility of some migration of pigment-forming cells from one feather follicle to another. Twelve years after it was discovered that the melanin pigmentation of feathers is a phenomenon dependent on highly autonomous migratory pigmentoblasts, Danforth concluded that these feather mosaics are truly pigment-cell mosaics, the product of two pigment cells that differ in genotype.

Another fixed potentiality in the skin at hatching is the responsiveness of the feather germ to sex hormone; for example, if the host is genetically male, the graft feather germ produces a contour feather that is structurally male, a form brought about by a hormonally altered type of morphogenesis.

The experimental production of genetic mosaics is the prototype of an extensive series of experiments designed to analyze the relative role of genes and hormones in the production of sex differences in feather pattern that is peculiar to each of the many well-defined races of the domestic fowl and to certain selected species of birds. Many racial traits are represented in the feathers—more properly in the feather follicles themselves, of whose reactions the fully developed feather is an index.

Several types or kinds of feather follicles (each bearing a papilla) * have been described by Danforth with respect to hormonal vs. genotypic regulation in the production of shape, color, and markings of feathers. The diversity of types of response is briefly characterized as follows: (*a*) feather follicles of either sex that produce sex differences in plumage by genic regulation without hormonal action (dove); (*b*) feather follicles that react to either male or female sex hormones; feathers produced in skin grafts follow the breed of the donor but the sex of the host (all breeds of the common domestic fowl—nine tested); (*c*) a feather follicle of each sex genotype that responds in its own way to both male and female humoral complexes; sex characteristics of the plumage are dependent on simultaneous action of both genic and hormonal factors (Reeves's and Ring-necked pheasants); and (*d*) a feather follicle of a hen-feathered genotype *(HH)* that produces a hen-feathered feather on a male Leghorn host (Silver Campine; no sexual dimorphism). A single gene difference is decisive for divergent reactions to hormone in two races, Campines and Brown Leghorn.

These four types of reaction of adult feather follicles to genes and hormones represent ways in which different forms of "protoplasm" (or tissues) respond to genetic and hormonal factors. The potentialities of protoplasm † are already fixed in

* At the base of the follicle is the feather papilla (or feather germ), a body comprised of a vascularized dermal component around which is a collar of epidermal cells from which the feather is generated.

† To Danforth the site of hormonal action is protoplasm, a term which to this writer is here equivalent to the prospective epidermal cells of the feather germ—cells that synthesize the protein keratin and provide the structural framework of the feather.

the skin transplant at hatching or, as stated by Danforth, "its future manifestations are rigidly pre-determined by hatching"; that is, protoplasm is under the control of intrinsic factors (genes, embryological factors such as interaction of tissue components). Genetic factors govern the course of fixation of the feather germ and seemingly the feather germ does not become fixed in regard to its sex. It is only later (toward sexual maturity of the host) that racial sex differences of the feathers are mediated by the endocrines. The feather germs have been prepared by gene action to respond to the hormone. Danforth emphasizes that responsiveness resides in the feather germ and not in the hormone. For example, in one kind of hormonal environment the feather germ produces a hen feather, in another kind a cock feather. The ability to respond to the hormone resides in the specific properties of the follicle papilla and not in the hormone.

As one of his finest contributions to developmental genetics, Danforth pioneered in establishing basic conditions for an understanding of the mechanisms for the production of sex differences in the plumage of birds. Of primary import is the concept that genes give character to the cytoplasm (of the feather germ) or "condition" it; that is, they determine the diversity of response in accord with racial differences in the genetic constitution of the bird. During development, a new adjustment comes about in the feather germ which imparts to it the capacity to utilize hormones in the making of sex differences not only in form but also, if genotype permits, in color marking of feathers.

As to the site of hormonal action, Danforth had little to say, save that hormones act as "activators or stimulators" and "produce their final effect only through such protoplasm as will respond to them." Moreover, the specificity of most hormone–tissue reactions is more properly an attribute of the tissue than of the hormone—it is largely a question of whether or not the tissue will utilize the hormone if available. To refer to hormones as chemical "messengers" is "more figurative than our present concepts should permit." Moreover, Danforth would agree that the term "target organ" should be replaced by a more appropriate term, the receptor organ (a functionally integrated unit) —better still, an interaction between hormonal molecules and receptor organ—a mutual fitting together of hormonal molecules and prospective epidermal cells, cells that synthesize keratin as they "build" the framework of the definitive feather. From this standpoint of original thought and interpretation, no one has excelled Danforth in presenting the characteristic features associated with feather follicles in the form of concepts that are not only original but still sound today.

On the question of the evolution of follicle types in birds having a sexual dimorphism of plumage, Danforth regarded the four types characterized by him as not corresponding to any particular evolutionary sequence; they do show, however, the kind of diversity that would provide for the evolution of special types of response. The phylogeny of the hormones presents a fascinating problem on which Danforth liked to think that the evolution of tissues had rendered hormones as necessary for their normal development and function.

In the foregoing appraisal, Danforth's scientific work has been centered on five major subjects: human heredity, the hair follicle, mouse genetics and mutation, genetic mosaics in birds, and the role of genes and hormones in feather characterization. An examination of his bibliography will reveal many papers on diverse subjects somewhat unrelated to the above major subjects. Many of these are singularly important yet only a few pages or a single paragraph in length. In his autobiographical sketch he wrote: "I suspect there may be those who would say that as an anatomist I am something of a geneticist, others who might think as a geneticist I am an amateur endocrinologist, and so on, but to me *all of my work seems to have a definite unity*" (italics mine). He points out further that the largest proportion of his projects never reached publication, for some were failures and some were just not completed. Danforth regarded the loss as slight, "for what one biologist does not do, some other one will" (a paraphrase of a saying by Professor Herbert S. Jennings of The Johns Hopkins University).

In an "epilogue" to his autobiographical sketch Danforth comments on research interests and motivations: "My natural inclination has been strongly toward leisurely *observation* (vs. exploration or experiment), and I have always aspired to put myself sufficiently *en rapport* with nature so that facts and relations would be perceived naturally (not 'logically'). Distant mountains, far streams and rare plants have a strong appeal, but there is even greater satisfaction in a more intensive study of what is within easy reach of a selected 'station,' whether near or far. In pre-college days I got a great deal of satisfaction out of studying various 'second crops' in plants but, despite some insight, I failed to recognize the full significance of the 'length of day' factor. For many years I observed conditions influencing venation in Sagittaria leaves, but never brought any study of the subject to completion. Every summer for over forty years I have given attention to the arrangement of leaves and floral parts in plants—with a good deal of intellectual satisfaction. . . . Despite a marked deficiency in musicality, I have a better 'ear' for bird notes than many of my friends who persist in trying to hear birds in terms of human musical notation, and I have gotten much enjoyment out of detecting varietal differences at the vocal level of, for example, the warbling vireos in different parts of the country. . . . I had early intended to devote myself to things like these, and to the profound enjoyment of such deeply spiritual beauty as there is in the notes of a hermit thrush projected against a background of receding thunder, or a chorus of white-throated sparrows singing in a spring twilight, with occasional interludes marked by the faint notes of a woodcock high in the evening sky. But while my orientation was basically to the out-of-doors, I early began studying nature in-doors, and have in a measure suffered the fate that Agassiz predicted for those that do so."

What was the fate that Agassiz predicted for those who study nature indoors and that Danforth, at the age of sixty-five, avows he had in a measure suffered? Louis Agassiz, the noted apostle of the *Great Book of Nature,* admonished his students to "read Nature not books," and explained to them, "If you study Nature in books, when you go out-of-doors you cannot find her." *

"You cannot find her" is a form of punishment that would have been very disquieting to Danforth. Actually, as noted above, his observations of nature continued throughout his life. Only in the sense of not having contributed significantly to the outdoors variety of natural history would he have been troubled. Occasionally he pondered on whether he would have arrived at some generalization broad in its scope had he remained an out-of-doors naturalist instead of an indoors naturalist.

The writer of this memoir now ventures to speak less formally, in the name of all Charles Haskell Danforth's friends, dead or living. We loved and respected him. What impressed us most, I think, was his quiet integrity. Had he been only a successful teacher and investigator, the writer does not think we would have responded so positively to his personality. But Danforth was different. He had both a mind and a heart. He was a

* See James D. Teller, *Louis Agassiz, Scientist and Teacher,* Graduate School Studies, Education Series No. 2 (Columbus, Ohio State University Press, 1947), p. 85. I am greatly indebted to a colleague of Charles Danforth, Dr. David Perkins of Stanford University, for his friendly interest and his thoughtful and painstaking research in locating the Agassiz quotation on which Danforth's comment is based. The quotation fits perfectly with Danforth's comment on his "natural inclination" to study nature outdoors. Also it is a distinct pleasure to acknowledge my indebtedness to Dr. Edward Lurie of the Milton S. Hershey Medical Center, Hershey, Pa., an authority on Louis Agassiz, for his keen interest and bibliographic aid in my search for the source and/or basis for the "in-doors–out-of-doors" philosophy of Danforth. In reading several publications on or by Agassiz suggested by Lurie, I was led by the key phase "you cannot find her."

devoted naturalist who built solid structures out of ideas. What he built will be consciously treasured in the memories of those who knew him. As Ralph Waldo Emerson said at the funeral of another naturalist, Henry David Thoreau:

> Wherever there is knowledge,
> Wherever there is virtue,
> Wherever there is beauty,
> He will find a home.

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KEY TO ABBREVIATIONS

Am. J. Anat. = American Journal of Anatomy
Am. J. Ophthalmol. = American Journal of Ophthalmology
Am. J. Phys. Anthropol. = American Journal of Physical Anthropology
Am. Naturalist = American Naturalist
Anat. Record = Anatomical Record
Arch. Dermatol. Syphilis = Archiv für Dermatologie und Syphilis
J. Exp. Zool. = Journal of Experimental Zoology
J. Heredity = Journal of Heredity
J. Morphol. = Journal of Morphology
Proc. 6th Internat. Congr. Genet. = Proceedings of the Sixth International Congress of Genetics
Proc. Soc. Exp. Biol. Med. = Proceedings of the Society of Experimental Biology and Medicine

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